

THE SOCIAL BIOLOGY OF ANTS¹

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If a capsule statement were required defining the prime significance of ants as research objects, it could be the following: the ants are a world-dominant taxon (family Formicidae) which have achieved their radiation by means of social modifications. They are unique in the magnitude of this achievement, being only remotely approached by their nearest competitors, the termites. With the ants, of which there are over ten thousand species, we are allowed to witness the employment of social design to solve the most diverse ecological problems ordinarily dealt with by single organisms. It is tempting to speculate (and perhaps impossible to prove) that these insects have employed all, or nearly all, of the social strategies permissible within the limits imposed by the hymenopteran brain and the peculiarities of their colonial system. In any case, the study of their social biology must still be considered in an early stage, notwithstanding an already large literature.

In the present coverage, emphasis will be on the past fifteen years, although there has been no hesitation to cite important earlier papers. For those interested, a historical perspective can be gotten by reading the books of Forel (53), Goetsch (58, 59), Richards (131), and Wheeler (185, 187). Only behavior and colonial organization are considered. Even after this restriction is made, certain topics have been omitted. Caste determination has been the subject of recent reviews by Brian (19) and Michener (115). Schneirla has summarized the results of his and his co-workers' well-known studies on New World doryline army ants in several detailed articles (140, 142, 143, 148), which should be consulted in conjunction with two more recent research reports (144, 145) on the genus *Neivamyrmex*. Especially useful are two of the reviews (142, 143) which take into account Raignier & Van Boven's treatise (128) on the African dorylines. Wilson (198) has considered early stages of army ant behavior in the primitive subfamily Ponerinae. In the present review, biological information in army ants has been mentioned where it was thought to have general significance. The special topic of fungus growing in the Attini has also been bypassed, in view of Weber's current publications (173, 174, 175), but other aspects of attine biology are covered.

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THE COLONY LIFE CYCLE

Mating.—The seasonal occurrence of the sexuals, the climatic conditions accompanying mating activity, and the behavior of the sexuals at the onset of the flights have received recent attention in detailed accounts by Geijskes (56), Kannoſki (80, 81, 83, 84), Marikovsky (114), and Talbot (163, 164), while fragmentary accounts on these subjects abound in the literature [e.g., review by Donisthorpe (45)]. Prior to the flights the workers dig supernumerary exit holes and the sexuals mill over the nest surface (3). Mating typically occurs in the air and is seldom seen. Some ponerines, the army ants, and the advanced social parasites are exceptional in mating on or near the nest (105, 141, 190, 202). In *Myrmecia regularis* Crawley, queens shed their wings in the nests and are fertilized on the ground outside by low-flying males, but other *Myrmecia* have more "normal" flights (72). Male swarms and copulation have been described in several non-parasitic myrmicine species by Brian & Brian (22), Kannoſki & Kannoſki (80, 84), and Wilson (195). Chapman (31) has gathered records of sexual swarms on the summits of mountains in the western United States and believes that these insects actively gather there to mate, a view supported by similar observations made by Collingwood (36) in England. The production and release of sexual forms in many species are timed in such a way as to enhance exogamy (114, 164), and it is tempting to accept the view of Scherba (135) that this represents organization shaped by natural selection at the interpopulation level.

The flights are species-specific in form and occur at predictable times of the day. The conventional view has been that one or more environmental factors, especially temperature and moisture, combine to trigger the behavior. Recently, however, McCluskey (111, 112) has demonstrated the existence of endogenous circadian activity in males of *Veromessor* and *Iridomyrmex* synchronous with the times of the nuptial flights. This points up the possibility that the environment is limiting instead of causative and suggests one important direction that future research on social behavior will take. Hodgson (74), for instance, has already cited indirect evidence that a persistent circadian rhythm initiates daily foraging in *Atta*. But not all castes conform: in *Iridomyrmex humilis* Mayr, at least, queens and workers lack persistent rhythms (112). The foraging of *Crematogaster scutellaris* (Oliver) workers is exogenously determined by temperature (149). Furthermore, the experiments of Grabensberger (65), purporting to prove a circadian time sense in ant workers, have been repeated by Reichle (129) and Dobrzański (43) with negative results. Jander's careful experiments (78) prove that *Formica* workers have a time sense which allows them to correct for the sun's movement in sun-compass orientation, but this does not add evidence for circadian rhythms, as Renner (130) points out.

The sperm stored in the spermatheca during the nuptial flight must last the lifetime of the queen and supply the ova for the entire worker

and virgin-queen population. Even with this in mind, Kerr's report (87) of 206 to 319 million sperm from mated queens of *Atta sexdens* (Linnaeus) comes as a surprise. S. Taber [in Moser (117)] has gotten similarly enormous counts of 65 to 111.5 million from queens of *Atta texana* (Buckley). In comparison, Mackensen & Roberts (113) estimated an average of 5.73 million sperm in mated honeybee queens. Kerr's estimates of 44 to 80 million sperm in the spermatophores of *A. sexdens* males indicate that multiple matings are the rule in this species. Multiple matings were directly observed, in fact, in another attine species, *Mycocepurus goeldii* Forel (87).

Colony founding.—From the extensive literature on colony founding in ants that has appeared in the past forty years [see reviews in (47, 60, 71, 83, 188)], it is possible to mention only a couple of points of special interest. It was discovered by John Clark and W. M. Wheeler [in (188)] that colony-founding queens of the primitive genus *Myrmecia* forage for prey to feed their first brood. In later detailed studies, Haskins & Haskins [(71, 72) and contained references] established that this "partially claustral" method is practiced throughout the primitive subfamily Ponerinae. One advanced ponerine, *Brachyponera lutea* (Mayr), was shown to be facultatively claustral (queen remains with first brood without foraging), thus completing the evolutionary series (70).

In many species of the higher ant groups, queens often band together in claustral colony founding ("pleometrosis"). Waloff (170) determined experimentally that queens of *Lasius flavus* (Fabricius) founding in groups survive better, lose less weight, and rear their first brood more quickly than those founding singly. The behavior of the temporarily parasitic species, whose queens invade host colonies to found their own colonies, has been the object of fresh studies by Kutter (96, 97) and Kanno-wski (83). Among their findings is the discovery by Kanno-wski that *Lasius speculiventris* Emery is a hyperparasite, i.e., it is a temporary social parasite on *Lasius minutus* Emery, which is thought to be parasitic on still other species of *Lasius*.

Thelytoky and alternation of generations.—Can unfertilized queens and workers produce female offspring? This was the subject of conflicting reports and opinions until 1945, when Haskins & Enzmann (69) showed rather conclusively that queens of *Aphaenogaster* can produce workers parthenogenetically. Since then, abundant experimental evidence has been gathered showing this capacity is present in both the queen and worker castes of the specialized myrmicine genus *Crematogaster* and formicine genera *Formica*, *Lasius*, and *Oecophylla* (7, 102, 103, 120, 152). However, these cases exhibit various degrees of facultativeness. Most ant genera studied outside the Formicinae exhibit the typically aculeate "Dzierzon's rule," albeit strictly with reference to fertilization versus nonfertilization and with no further cytological implication (104).

In detailed studies of the biology of *Oecophylla longinoda* (Fabricius),

including a cytological analysis of gametogenesis, Ledoux (102, 103, 104) has demonstrated a hitherto unsuspected alternation of generations. The queens lay eggs that vary little in size and conform to the aculeate rule: if fertilized they produce workers, if unfertilized, males. Workers lay two sizes of eggs, one with about the diameter of a queen-laid egg (1 mm), the other only about half as wide (0.6 mm). The larger worker-laid egg is produced precociously, before it accomplishes the maturation division, but its first division in embryonic development is reductional (to $n \approx 12$). These eggs become males. The smaller egg is produced when the oöcyte is retained in the oviduct until division takes place, but this division is equational, and later divisions are also equational, so that the product is a diploid queen or worker. Workers laying the latter type of egg are treated like queens in the nest and are important supplementary reproductives, in addition to being the sole source of true queens. Queen production by queens has not yet been demonstrated. It may be that they emit some kind of selectivity inhibiting stimulus effective in larval development, as Brian (20) has suggested. On rather limited evidence, Soulié (152) has hypothesized a similar cycle in *Crematogaster*.

Later development.—The subject of colony growth has received the attention of many recent authors [reviews in (3, 10, 18)], but the most complete work is that of Brian (12, 13, 18, 21) and Weir (179, 180) on *Myrmica rubra* (Linnaeus) and *M. ruginodis* Nylander in Britain. A few points are especially noteworthy. Colony growth is only roughly sigmoidal. About seven years is required to add 300 workers; then a spurt of growth in two years adds about 600 workers and the first winged queens. After this, the effusion of sexuals and limited egg productivity of the queen brakes further growth and causes erratic fluctuation in colony size. The production of eggs and pupae reach two simultaneous peaks that occur in early and late summer, respectively. The number of larvae dips at the earlier, larger egg-pupa peak. Thus, a brood cycle is defined paralleling the well-known *Eciton* cycle described by Schneirla (140). The immatures become dormant as third-instar larvae late in the summer. They are brought into this condition by the workers, which undergo certain physiological changes late in the season, but whether they are in true diapause has not been determined. The workers themselves do not enter diapause, which is also the rule in other ant species [with the exception of at least some *Camponotus* (75)]. The yearly cycle is neatly adjusted to the stresses of the cold-temperate environment and timing of the rearing of the sexual castes (19, 21).

COMMUNICATION

The greatest advances in this subject have been made exactly in the direction most expected, namely in the identification of the chemical stimuli of social behavior. Until the 1950's, students of ant behavior conceded a major role to chemical secretions but devoted their analyses mainly to the more easily seen tactile stimuli, a trend culminated in the elaborate

antennal ("Fühlerschläge") code postulated by Wasmann in 1899 (171). More recent authors [e.g. (58, 59, 107, 138, 142, 155)] adduced evidence from behavioral and morphological studies that suggested the existence of elaborate systems of chemical releasers, but were not able to identify discrete substances. In the past four years, the isolation and identification of the pheromones and the location of their glandular sources has begun. The greatest progress has been made on the trail and alarm substances, as shown in Tables I and II.

TABLE I
SOURCES OF TRAIL SUBSTANCES IN ANT SPECIES

Species	Glandular Source	Dispensing Organ	Authority
MYRMICINAE			
<i>Solenopsis geminata</i> (Fabricius), <i>S. saevissima</i> (Smith), <i>S. xyloni</i> McCook	Dufour's gland	sting	Wilson (199, 200)
<i>Pheidole fallax</i> Mayr	Dufour's gland	sting	Wilson (203)
<i>Acromyrmex octospinosus</i> (Reich)	true poison gland	sting	Blum (9)
<i>Atta cephalotes</i> (Linnaeus), <i>A. texana</i> (Buckley)	true poison gland	sting	Blum and Moser (9)
DOLICHODERINAE			
<i>Iridomyrmex humilis</i> Mayr, <i>I. pruinosus</i> (Roger)	Pavan's gland*	posterior border of abdominal sternite VI	Wilson & Pavan (208)
<i>Monacis bispinosa</i> (Olivier)	Pavan's gland*	posterior border of abdominal sternite VI	Wilson & Pavan (208)
FORMICINAE			
<i>Paratrechina longicornis</i> (Latreille)	hind-gut	anus	Wilson (203)
<i>Lastus fuliginosus</i> (Latreille)	hind-gut?†	anus	Carthy (27)

* It is proposed here to use the term Pavan's gland to refer to the *organo ventrale* discovered in the Dolichoderinae by Pavan (121), in order to distinguish it from other ventrally located glands in the worker ant and to avoid further confusion with the ventral gland of the Orthoptera. See Miradoli Zatti & Pavan (116), Pavan & Ronchetti (123), and Wilson & Pavan (208) for morphological details.

† See explanation in text.

Odor trails.—Quite a new picture of the nature of trails has been obtained. It is now necessary to distinguish between "exploratory" trails and "recruitment" trails. The former are found in legionary (army ant) species among the Ponerinae and Dorylinae (137, 140, 197), and are laid more or less continuously by foraging workers. The contribution of the single worker appears to be relatively slight, but the accumulated contribution of the foraging columns is heavy enough to last for days or even weeks (141, 146, 197). To date, the glandular source of exploratory trail substances remains unknown. On the other hand, the recruitment trails are laid only by workers that are returning to the nest following the discovery of food, lost nest mates, superior nest sites, etc. They can be ephemeral or built up by accretion into persistent "trunk routes" (162). They are typical of the trail-laying Myrmicinae, Dolichoderinae, and Formicinae. In the cases thus far analyzed (Table I), the recruitment trail substances have proven to be strong attractants. Although most authors

as late as 1957 (161, 168) thought that the returning workers provided additional stimuli (probably tactile) that induced others to follow the odor trail, it is now clear that the trail substance suffices to release the entire follower response (200). The attractant is emitted in invisible streaks. In the fire ant, *Solenopsis saevissima*, the Dufour's gland reservoir contains no more than 0.005 ml of the substance, and a single worker has been estimated to pay out between 4×10^{13} and 2.4×10^{15} mol/cm of trail (204). The concentration in threshold of response was further estimated to fall between 2.4×10^{13} and 1.4×10^{15} mol/ccm. When laid on a glass surface, the fire ant trail substance diffuses to attain a maximum effective width of about 2 cm; the effective diameter then diminishes to zero in about 100 seconds. Wilson's analysis (200) shows that as a result single workers are unable to communicate over distances greater than 50 cm, and longer trails must be built up in chain fashion by multiple workers. An odor trail laid by one worker conveys four bits of information with respect to direction and two bits with respect to distance, or the equivalent of pinpointing one of 16 equiprobable sectors of a compass and one of four equiprobable intervals of a distance scale. Interestingly, this is about the same amount of information communicated with respect to direction and distance by the honeybee waggle dance. The amount of material laid per unit time, as measured by the application time, evidently does not vary greatly with quality or quantity of the food source. This characteristic, plus the rapid evaporation and diffusion of the trail substance, requires the colony to employ "mass communication" in determining the number of workers that go forth. Specifically, the number of workers leaving the nest increases with the amount of pheromone in the trail, the amount of pheromone increases with the number of workers laying trails in unit time, and the number of trail-layers increases with the quality and quantity of the food find. The first studies suggest that among most members of the subfamilies Myrmicinae and Dolichoderinae, as well as in the formicine *Paratrechina longicornis* (Latreille), trail-laying appears to resemble the fire-ant type. In some *Myrmica* and *Lasius*, on the other hand, workers lay visible streaks of material (27, 110). In the case of *Lasius fuliginosus* (Latreille), Carthy (27) showed that the bulk of the "odor spot" comes from the hind gut, but his experiments were not designed to distinguish the action of the pheromone that almost certainly occurs in the trail. Carthy succeeded in disproving (for *Lasius*) the use of a kinaesthetic sense in orientation and polarization cues in the trail, thus refuting the old frequently discussed hypotheses of, respectively, Piéron (126) and Bethe (6), as well as weakening Forel's rather vague theory of the "topochemical sense" [perception of form through odor distribution (53)]. Parallel results were obtained in the study of *Solenopsis saevissima* just mentioned.

Recruitment trail substances, when extracted and tested with the artificial trail assay, have proven to be mostly species-specific, even among species belonging to the same genus (200, 208). No trail substance has

yet been chemically identified. Cavill & Ford (28) noted that workers of *Iridomyrmex detectus* (Fr. Smith) follow trails of 2-methylhept-2-en-6-one extracted from other *detectus* workers, but no conclusion can be drawn from this result in the absence of a quantitative bioassay. In a like manner, Blum and Wilson [in (9)] found that *I. pruinosus* (Roger) workers weakly follow trails of 2-heptanone, the natural alarm substance produced by the anal glands; but the response to the contents of individual anal glands is far less than that to the contents of a single Pavan's gland, which must be regarded as the source of the true odor trail. The notion, occasionally encountered in the literature [e.g. (85)] that workers of the *Formica rufa* group lay trails of formic acid, is without foundation. Stumper (158) has recorded a new unidentified odorant in the poison gland secretion which he suggests may be the trail substance, but no behavioral tests have been made, and the new chemical may equally well be a defensive agent working with formic acid. In *Acanthomyops* we may note that citronellal functions as a spreading agent for formic acid (57), while in *Tapinoma nigerrimum* (Nylander) iridodial traps and slows the evaporation of methylheptenone and propyl isobutyl ketone (124).

Alarm substances.—This category covers a variety of substances, apparently mostly terpenoids, with various behavioral effects. The expression "alarm" is only loosely appropriate. In *Pogonomyrmex badius* (Latreille), the pheromone is an attractant at low concentrations. At high concentrations it acts as an excitant, releasing the typical aggressive posture and circular running of alarm behavior, and when exposed to workers for long periods of time it causes directional digging behavior (11, 196). In *Atta rubropilosa* Forel, the alarm substance citral causes attack on the source of emission (26); a similar response is caused by the alarm substances of the New World army ants (25) and the Australian legionary ponerine *Onychomyrmex hedleyi* Emery (203). In dolichoderines the response (in some species) consists of attraction at low concentrations and attack and milling at higher concentrations. In *Tapinoma sessile* (Say), colonies exposed to prolonged dosages emigrate (208). Unlike trail substances, the alarm substances are not usually species-specific.

A few of the alarm substances have been chemically identified, as indicated in Table II. Many of the other ant secretions identified by Pavan, Cavill, and their associates [see (29, 122, 124) with contained references] will undoubtedly prove to have the same function when behaviorally tested. For instance, methylheptenone and propyl isobutyl ketone, identified in *Tapinoma nigerrimum*, are fully effective as alarm releasers in *T. sessile* (208). On the other hand, the more complex ant secretion iridomyrmecin (from *Iridomyrmex humilis*) has thus far proven behaviorally inert (203) and probably functions primarily as a biocide, as Pavan suggested originally. At least two substances, citral and citronellal in *Acanthomyops claviger* (Roger), serve both functions (30, 57). Finally, pure alarm substances applied in laboratory tests elicit the full

TABLE II
ALARM SUBSTANCES IN ANTS

Species	Chemical	Glandular Source	Authority
PONERINAE			
<i>Pachycondyla harpax</i> (Fabricius)	?	mandibular gland	Blum (9)
<i>Paraponera clavata</i> (Fabricius)	?	mandibular gland	Wilson (203)
DORYLINAE			
<i>Eciton hamatum</i> (Fabricius)	?	head (mandibular gland?)	Brown (25)
<i>Nomamyrmex esenbecki</i> (Westwood)	?	head (mandibular gland?)	Brown (25)
<i>Labidus praedator</i> (Smith)	?	head (mandibular gland?)	Brown (25)
MYRMICINAE			
<i>Apha sexdens rubropilosa</i> Forel	Citral	mandibular gland	Butenandt, Linzen & Lindauer (26)
<i>Pogonomyrmex badius</i> (Latreille)	?	mandibular gland	Wilson (196)
<i>Solenopsis saevissima</i> (Smith)	?	head	Wilson (200)
DOLICHODERINAE			
<i>Iridomyrmex pruinosus</i> (Roger)	2-heptanone*	anal gland	Wilson & Pavan (208)
<i>Tapinoma sessile</i> (Say)	?	anal gland	Wilson & Pavan (208)
<i>Monacis bispinosa</i> (Olivier)	?	anal gland	Wilson & Pavan (208)
<i>Liometopum occidentale</i> Emery	?	anal gland	Wilson & Pavan (208)
FORMICINAE			
<i>Lasius fuliginosus</i> (Latreille)	β (4:8-dimethylnona-3,7 dienyl) furan (=dendrolasin)	mandibular gland	Pavan (121)
<i>Acanthomyops claviger</i> (Roger)	citronellal, citral (9:1 proportion)	mandibular gland	Ghent (57)

* Identification by M. S. Blum.

natural responses. Tactile and auditory stimuli probably play some role in alarm communication, but this increasingly appears to be a secondary one.

Other pheromones—Stumper (156) has demonstrated that queen attractants of certain species can be transferred to "dummy" queens of elder pith and still induce the well-known worker responses of clustering, licking, and transport. Wilson (200) reported the extraction of a substance from worker fire ants that causes grooming behavior. A gaseous product, probably carbon dioxide, was also found to attract and settle fire-ant workers. The removal of worker corpses from the nest is caused entirely by perception of certain decomposition products, notably long-chain fatty acids and their esters (207). Francfort (54) has described an experiment which indicates that a chemical stimulus is responsible for the well-known phenomenon of social facilitation among workers. [For a review of the literature on facilitation in ants, see (139).] Larvae almost certainly produce pheromones peculiar to themselves. Their surface attractants are well known. Also, the hungry larvae of some species apparently produce chemical cues that guide nurse workers to their mouthparts (107, 203). It is possible that larvae also discharge excitants that induce

foraging in workers. For instance, Lappano (101) found that in the army ant, *Eciton burchelli* (Westwood), the labial glands reach maximal development in all larval size groups at the beginning of the peak of raiding activity which occurs on the eighth or ninth nomadic day. This line of evidence is suggestive, but as Lappano indicates, its behavioral significance, if any, must be explored by experimentation.

The accumulated evidence has led to the view that most social behavior in ants is mediated by chemical releasers which are discharged at appropriate times from exocrine glands and cause stereotyped responses (196). It has indeed been proven possible to bioassay some of the substances by inducing the reactions *in vacuo*. But the deciphering of the chemical code has scarcely begun, and we seem to be entering "a field of research extremely interesting and varied, which will henceforth prove rich in information and abundant in surprises" (155).

Queen and soldier control.—When the queens of *Formica pratensis* Retzius are removed, the workers after a time (*a*) lay an increased number of eggs; (*b*) in certain times of the year rear sexual forms (7, 8). Twelve to 20 hr after the queen of *Eciton* is removed, the colony will readily fuse with another, queen-right colony. If deprived longer, the bivouac organization deteriorates (148). Bier (8) has proven that in *Formica pratensis* the queen odor is not responsible for suppression of the workers and that the inhibiting effect is distributed by the workers. His hypothesis is that the queen appropriates from the workers salivary-gland secretions [labial?, see (64)] that would otherwise contribute to worker fertility. The parallel with the queen substance of the honey bee is obvious, as Karlson & Butenandt (85) point out. Schneirla & Rosenblatt (148) favor a pheromone hypothesis in the case of *Eciton*. Brian & Carr (23) showed that in *Myrmica* the presence of the queen affects larval growth by causing an earlier start, an improved survival, a smaller pupal size, and a diminished production of queens. The possibility of queen-larvae competition was experimentally ruled out, and these authors present an exhaustive list of remaining hypotheses. A parallel inhibitory effect was found in *Pheidole morrisi* Forel by Gregg (66), who showed that soldiers inhibit to a limited extent the production of more soldiers. Gregg hypothesized but was not able to prove the existence of an inhibitor substance. At this point perhaps the most likely approach to the problem of caste control would be a direct test of the inhibitory pheromone hypothesis.

Colony odor.—It has long been known that in some species alien colonies can be freely mixed without a sign of hostility, whereas in others intercolonial hostility is shown. In the latter case, the survivors habituate to each other and in time acquire the same colony odor. The source and nature of such a highly specific odor has long been a mystery. Recently, Soulié (151) presented indirect evidence indicating that in *Crematogaster* the odor might be derived from the nest itself. This still left unanswered the question whether the ultimate source of the nest odor derived from

the nest material itself or from accumulated secretions originating in the ants. A partial answer has been supplied by Lange (98, 100). He introduced a sensitive technique: utilizing rate of food transmission as an index of the affinity of workers of *Formica polyctena* (Förster) mixed under experimental conditions. When colony fragments were separated and maintained under identical conditions and then recombined, the intergroup rate of food transmission did not differ from the intragroup rate. However, when the fragments were given different diets or placed in different nest material for awhile, the intergroup rate dropped. Withholding of queens, the multiplying of queens, and the introduction of alien queens had no effect. Lange's conclusion that the behavioral changes were due to alteration in nest odor which, in turn, was caused by the change in chemical environment, is a reasonable one. Thus, with ants as well as with honeybees, dietary differences play an important role (79).

Auditory communication—Sound production and hearing in ants has been partially reviewed by Haskell (67), but some further comments are needed here. Although stridulation is widespread in ants, and what appear to be stridulatory surfaces even occur in larvae [leading Wheeler & Bailey (189) to speculate on the possibility of communication in some taxa], little evidence has been adduced for the existence of sound communication. On the basis of careful experimentation, Autrum (2) and Haskins & Enzmann (68) found perception of aerially-borne sound rather weakly developed in ant workers, although perception of solid-borne vibration is acute. In the genus *Myrmica*, Autrum could find no evidence that stridulation functions in recruitment or alarm. Workers ordinarily stridulate only when their freedom of movement is restricted, and this apparently has no effect on nearby sister workers. An elaborate sound-producing organ, including a distinctive muscled vibrator and resonator chambers, was described in *Plagiolepis*, *Leptothorax*, and *Solenopsis* by Nachtwey (118), who used this morphological evidence to postulate sound communication in ants. However, Nachtwey's organ appears (to the present reviewer, who re-examined *Plagiolepis* and *Solenopsis*) to be based on a misinterpretation of articular structures in the propodeum and anterior petiolar peduncle and of the atria of the well-known metapleural (= metasternal) glands. [For complete descriptions of this portion of the body detailing the histology of the metapleural glands in various species see Pavan & Ronchetti (123), Tulloch (167), and Whelden (191, 192, 193).] Field evidence on sound communication is meager. Collart (35) reported that when a worker from a raiding column of *Megaponera foetens* (Fabricius) was trapped in sand 50 cm from the column, it stridulated audibly until it was excavated by other workers drawn to the spot. It is premature, however, to conclude that the rescuers responded to the sound. Exactly the same response is released by the mandibular gland secretion of *Pogonomyrmex badius* (196), and a disturbed *Megaponera* worker may discharge an alarm substance with

similar effect. Other myrmecologists have noted that workers of certain tropical arboricolous *Camponotus* and *Polyrhachis* tap their heads violently on the nest walls when disturbed, but this is not necessarily a form of communication. In fact, no evidence has yet been adduced to establish firmly the function of sound production in ants. It could be primarily or even wholly defensive.

FOOD EXCHANGE

Regurgitation.—Wallis (169) has provided an ethological analysis of food sharing in *Formica* which somewhat alters our understanding of this phenomenon. Antennal and foreleg palpation are used by donors and acceptors alike. Foreleg palpation is indicative of strong motivation and occurs more frequently in the acceptor, other things being equal. Whether a donor or acceptor initiates the exchange depends on the relative strengths of the motivation of the two participants. A worker group can be shifted from predominantly soliciting behavior to donor behavior merely by feeding it to satiation. That antennation is not always a necessary precursor of regurgitation has been noted in Stumper's study (159) of *Proformica nasuta* (Nylander).

In a masterful comparative study of the ant proventriculus, Eisner (48, 49) showed how this structure evolved in ants to serve as a selective reservoir of the crop contents. The elaborate sepal and dome-shaped structures so useful in the classification of the Dolichoderinae and Formicinae apparently are designed to provide automatic, primarily nonmuscular valves to withstand mounting fluid pressure in replete workers. In a later study, Eisner & Happ (50) interpreted the infrabuccal pocket as a means of filtering solids that would otherwise clog the narrow, rigid proventricular channels.

A recent interesting discovery is that, contrary to earlier belief, some of the most primitive ant genera, e.g., *Ponera* and *Myrmecia*, practice regurgitation (73, 106). Gösswald & Kloft (64) recorded food exchange in every one of a wide range of European species studied, including *Ponera*. Thus, the behavior pattern appears nearly universal in the Formicidae. Exceptions to the rule include the myrmicine harvester *Pogonomyrmex badius* (203) and members of the primitive genus *Amblyopone* (73).

Using radioactive tracers, Gösswald & Kloft (62) and Eisner & Wilson (51) independently arrived at two new quantitative conclusions. First, in species with rapid regurgitation rates, such as many of the Formicinae, the sugar solution stored in the crop of a single foraging worker may be evenly distributed (in a Gaussian manner) to workers in groups of a hundred or more in as little as 20 hr. Second, very little, if any, of the ingluvium is given to queens and larvae. In a later paper, Gösswald & Kloft (64) proceeded to describe liquid food exchange in impressive detail. They found that the tracer substance (P^{32}) finds itself after 24

hr from the crop to the labial glands, whence it is passed to the queen and larvae, thus proving for the first time that a different diet is employed in the ant colony. Some of the material is passed from the larvae back to the workers. The sharply defined optimal temperature range of 24° to 26° C for regurgitation in *Formica polyцена* was demonstrated. Also, these authors made first measurements on exchange between host species and various species of social parasites, with a resulting demonstration of the gradual evolutionary loss of ability to donate among the more advanced parasites. Some exchange was recorded among various species of the *Formica rufa* group, and a similar result was obtained in the field by Chauvin et al. (33); the significance of this anomalous result is unclear. Stumper (159) used the same tracer technique to study the behavior of the "honeypot" repletes of *Proformica nasuta*. His results go far to resolve the long-standing controversy about the adaptive significance of the replete caste [see review by Creighton (37)]. At moderate temperatures, food passes chiefly from foraging workers to the repletes, but at 30° to 31° C, when the metabolic needs of the colony sharply increase, the direction of flow is reversed. Stumper infers that in nature the communal supply in the crops of the repletes is built up in relatively cool, moist weather and tapped in hot, dry weather. These results partially explain why, as Forel (52) first pointed out in 1902, most of the species that produce extreme repletes are also desert dwellers. Kanno (82) and Riordan (132) have employed radioactive tracers in the field to locate and circumscribe colonies of *Lasius* and *Camponotus*.

Trophic eggs.—It has long been known that workers of many ant species have well-developed ovaries, but the eggs were not thought to have any social function. In his definitive histological study, Weyer (184) suggested that in some unexplained manner the eggs were resorbed to provide added "vitality" to the workers generating them. Now it is known that worker-laid eggs are commonly used as food for the queens and larvae. Brian (15) and Weir (178) found this to occur occasionally in *Myrmica rubra*, and Wesson (183) and LeMasne (107) recorded cases of it in *Leptothorax*. Older mother queens and young larvae of *Pogonomyrmex badius* are fed exclusively with modified worker-laid "trophic eggs," while, in the primitive genus *Myrmecia*, trophic eggs are also solicited and eaten by adult workers during the winter (55, 203). Bazire-Benazet (4) reports the production of "omelets" of fused trophic eggs by *Atta rubropilosa*. The "trophallactiques proctodeaux" described in several dolichoderine genera by Torossian [(166) and contained references] is almost certainly the same phenomenon, judging from his descriptions and photographs.

POLYETHISM

Weir (176) has used the term "polyethism" to mean, in a rather special sense, the differences in "job preference" among worker ants.

Actually, the term would be quite useful if more broadly employed as a synonym for the cumbersome "division of labor," and a distinction made between "age polyethism" and "caste polyethism."

Age polyethism.—It has long been known that ant workers, like honey bees, remain in the nest as nurses for a time after eclosion and commence foraging as they age. Weir (176), for instance, found that *Myrmica scabrinodis* Nylander workers eclosed during the current season tend to serve as nurses, those produced in the previous seasons as nest builders, and older workers, possibly two years old, as foragers. Wide individual quantitative differences in this polyethic sequence occurred, with the domestic period proving the most plastic. In *Myrmica rubra*, marked variation among workers was detected in locomotor activity, behavior, and metabolic activity, which Weir suggests is correlated with age differences (177). Otto's monograph (119) on *Formica polyctena* (= *F. minor*) gives the most thorough picture of age polyethism in a single species to date. Workers remain in the nest for about the first forty days, during which time their ovaries become well developed (and presumably functional—see "Food Exchange" in this review). Then, as the ovaries regress, the workers commence their *Aussendienst* as foragers and nest builders. Great variation in this sequence and in the specific labor performed exist among individuals; for instance, many never serve as nurses. Histological studies show that beside the ovaries, several of the major exocrine glands undergo predictable age changes. Otto is thus able to provide some valuable first clues as to their possible social functions.

Caste polyethism.—As just noted, individual differences exist in the sequence of age polyethism. In worker-monomorphic species there may be no correlates in morphological variation, and the polyethic classes that are distinguishable after adjustments are made for age are sometimes referred to as "physiological castes" on the sound assumption that underlying physiological differences do exist. Where true morphological subcastes exist within the worker caste, caste polyethism is invariably pronounced. The latter phenomenon has yet to be studied in any thorough manner, but a few recent findings are noteworthy. In *Formica obscuripes* Forel (= *rufa melanotica* Emery), the size-frequency distribution is unimodal but a dramatic polyethism exists: smaller workers forage for honeydew, and larger ones tend the nest and collect the honeydew in the field from the minors through regurgitation (89). In the "honey ant" species belonging to diverse formicine genera it is generally the largest workers which develop into repletes (157, 203). In *Oecophylla longinoda* (Fabricius) and *Daceton armigerum* (Latreille), on the other hand, it is the minor workers which remain in the nest while the majors forage (103, 172, 201). In most ant genera with a highly modified "soldier" caste, these individuals function primarily in colony defense, but the defensive behavior employed varies radically (38, 39, 40, 140, 194). Thus,

polymorphism cannot be said to be linked to polyethism in any simple, consistent way among the ant taxa.

ERGONOMICS

The term "ergonomics" is borrowed here from human sociology to give some formal recognition to a trend of research which is destined to become increasingly important in the study of social insects. In our context it is intended to mean the study of labor productivity and efficiency in the insect colony. A great deal of information of this kind is, of course, already available for the honey bee, and a start has been made in the social wasps with Deleurance's analyses (41) of work in the *Polistes* colony. No firm principles have yet emerged pertaining to ants, but data are accumulating to this end. Pickle's measurements of territories, biomass, and earth-moving in British ants [(125) and contained references] have been frequently cited in the general ecological literature. Some of his figures suggest nicely the large amount of work performed by ant colonies; for instance, single *Lasius flavus* colonies, while occupying average areas of about 50 square yards, used about 330 g of earth per year in nest building. Holt (76), in an analysis of foraging activity of a mature *Formica rufa* Linnaeus colony, calculated that on one typical day, 60 to 70 thousand workers, weighing 700 g, made 300 thousand foraging trips to collect at least 800 g of food, of which 44 per cent was honeydew. Stumper (159) measured the crop content of a replete *Proformica nasuta* as 10 mg; in laboratory colonies this supply is doled out to about 100 sister workers over 30 days, or at the estimated energy rate of 0.04 calories per worker per day.

In three novel and stimulating papers, Brian (14, 16, 17) has set out to measure the efficiency of brood rearing in *Myrmica rubra*. Three causes of inefficiency were demonstrated: (a) large larvae so monopolize food input from the workers that they cause a suboptimum distribution; (b) the larvae are massed in such a way that they prevent the most direct servicing by the greatest number of available nurses; (c) the larvae receive food through a trial and error method rather than by transmitting a "hunger" signal. Given the first two suboptimal relations as stable conditions, Brian calculated the optimal worker-to-larva ratio and found it to be close to the natural ratio. Inefficiency was defined by the author in this system without reference to other biological phenomena. The possibility remains that the "defects" described provide advantages to the colony in other unforeseen ways that outweigh the disadvantages in larva rearing, and it cannot be concluded that larva rearing is perfectable without other alterations in social structure. Brian has pointed the way for making such estimates in a quantitative manner.

NEST MICROCLIMATE REGULATION

The ant colony has very marked environmental preferenda and attains them by two primary means: nest construction effective in regulating the

microclimate, and movement of the colony within the nest or to new nest sites. As a rule, the more elaborate the nest architecture of the species, the less mobile are the colonies. The mound nests of *Pogonomyrmex* and *Formica* have been extensively analyzed by several myrmecologists with respect to microclimate regulation [(34, 86, 127, 134, 135, 136, 153, 181, 209) and contained references]. It is clear in the species studied that mound construction provides higher nest temperatures. Several authors claim further that in the *F. rufa* group the mound temperatures, especially about 20 to 30 cm beneath the surface of the mound apex, vary less than those of the surrounding air and soil and stay consistently close to the ant preferenda (86, 127, 153). In *F. ulkei* Emery, on the other hand, the mound temperatures merely remain higher, and they fluctuate more widely than in the surrounding soil (136). In both cases, the preferenda temperatures are almost always maintained somewhere in the nest, and the brood are shifted accordingly. Moisture regulation in *F. ulkei* is more dramatic. Relative humidity of the nest chambers is much less variable in comparison with that of the surrounding soil, and the grand mean weekly content coincides with the brood preferendum [that is, the zone in which the workers prefer to place the brood (134)]. The workers of *Formica* adjust the mound structure in response to changes in soil drainage and shading and expertly repair major damage (32, 99, 134, 165). Curiously, the *Eciton* army ants show parallel regulation within the bivouacs formed mostly of masses of their own bodies (77, 147). With the recording of these important facts, it must be admitted that very little of concrete value is known about how the regulation is achieved. Some of the phenomena seem logically adaptive, e.g., the mounds are slanted apparently to catch more sunlight, the sponge-like structure of the upper gallery systems seem to provide better insulation, and the exits are open and shut apparently correctly for favorable moisture control. Zahn (209) has even claimed that in cool weather the nests of *F. rufa* are significantly warmed by the return of workers who sun themselves outside the nest. This *Wärmeträgertätigkeit* is suggested to be a new kind of stereotyped social behavior. These various features have been subjected to very little experimentation, however. The analytical micrometeorology of ant nests is still a largely undeveloped subject, as Scherba (134) has recently made clear.

SOCIAL PARASITISM

A rich variety of new parasitic species, representing almost every conceivable evolutionary stage, have been added since the time of Wheeler's general account (185). Reviews of several of the more important parasitic taxa are available (24, 90-93, 95, 96, 154, 202). "Emery's rule," that permanent parasitic species are phylogenetically very close to the host species, has been upheld by the new finds, as noted by Brown (24) and Stumper & Kutter (160). Most of the species have continued to turn up in North America and Europe (where ant collectors are the most dili-

gent), but at least two have been discovered in New Guinea rain forests (205), while Kusnezov (90, 91, 92) has described many new parasitic myrmicines from temperate South America. A few other species have been found in Africa and Australia (24).

The "ultimate stage" in permanent social parasitism has been added with the discovery by Kutter (94) and Stumper (154) of the European myrmicine *Teleutomyrmex schneideri* Kutter, a parasite of *Tetramorium caespitum* (Linné). Like most permanent parasites, this remarkable ant lacks the worker caste. The queens are quite small and have flattened bodies and curved, incrassate legs—all aberrant adaptations which allow them to fasten themselves onto the bodies of the host queens. Gösswald's histological study (61) shows that the body of the *Teleutomyrmex* has undergone extreme degeneration. Mouthparts, the sting, the central nervous system, and various exocrine glands are all notably reduced. The metapleural gland is missing, thus breaking the one anatomical character that in the past seemed to be absolutely diagnostic for the Formicidae.

The earliest evolutionary stages of permanent social parasitism have been described by Wilson & Brown (205, 206). In *Monomorium metoecus* Brown and Wilson, the worker caste is still present and, on first examination at least, appears fully functional. In *Kyidris yaleogyna* Wilson and Brown workers are present in abundance but their behavior is somewhat degenerate. LeMasne (108) has supplied the remaining steps in *Plagiolepis*. In *P. grassei* LeMasne, the workers are scarce and appear only after the sexuals, a unique reversal of the usual order in ants. In the closely related *P. xene* Staercke, the worker caste has disappeared altogether. LeMasne (109) has found the two species together in one nest of the host *P. pygmaea* (Latreille), thus making the first record of true double parasitism in nature.

Douglas & Brown (46) have described *Myrmecia inquilina* (subfamily Myrmeciinae), the first true parasite among the lower ants. Parasitic species are now known from all major subfamilies except the Ponerinae and Dorylinae.

King & Sallee (88) have recorded the puzzling occurrence of mixed colonies of *Formica clivia* Creighton and *F. fossiceps* Buren. Both workers and sexuals of both forms are produced. King & Sallee have considered the alternative possibilities that the two forms are either (a) genetic morphs or (b) distinct species linked in an aberrant symbiosis. The field data are inconclusive. The case deserves further attention in view of the more recent, surprising evidence that food is transmitted in natural conditions among species of the *F. rufa* group (33).

The slave-making species of *Polyergus* and the *Formica sanguinea* group have been the object of several important behavioral studies (5, 42, 44, 133, 165). Dobrzańska & Dobrzański (42, 44) in particular have apparently solved the classic problem of how the raids are organized. There are no scouts or raid leaders, and any individual or small group

of individuals can be removed at any time without impairing the raid. The host nests are apparently discovered and learned individually by a relatively large number of "activator" workers who induce others to attack in a given direction. Arnoldi (1) has recorded unusual raiding behavior in the little-known Russian slave-maker *Rossomyrmex proformicarium* Arnoldi. The workers run in pairs, one individual carrying another over its head, and proceed to the raiding area in a loose file. The details of dulotic behavior of the myrmicine slave-maker *Harpegoxenus americanus* (Emery) were reported by Wesson (182). Compared with the formicines, the colonies are quite small and the raids loosely organized, in some cases being conducted by only a single individual. Unlike the formicines, the raiding parties are guided by odor trails. In many cases the workers settle in the raided nests and commence satellite colonies. The morphologically less specialized slave-raider *Leptothorax duloticus* Wesson, also a myrmicine, behaves in an essentially similar manner (183).

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